

## CROP MILK AND CLUTCH SIZE IN MOURNING DOVES

DAVID E. BLOCKSTEIN<sup>1</sup>

**ABSTRACT.**—Doves are unique among birds in producing crop milk and in having a determinate clutch size of 1-2 eggs. In North Dakota, 97.2% of 1203 Mourning Dove (*Zenaida macroura*) nests had 2 eggs. Clutches of 3 (N = 24) and 4 (N = 4) eggs probably were laid by more than one female per nest. Experimental additions of a second egg to incomplete clutches and removals of the second egg from recently completed clutches verified that Mourning Doves are determinate layers. To examine the role of crop-milk production as a factor that limits clutch size, a third nestling was added to nests of Mourning Doves during (early addition: 3-E) and after (late addition: 3-L) the period of complete dependence on crop milk. All three young fledged at 31% (3-E) and 42% (3-L) of these nests. Growth rates were significantly reduced for 3-E nestlings relative to normal broods of 2; growth rates of 3-L broods were intermediate. Crop-milk production is apparently an important reason why the clutch size of doves (Columbidae) is not more than two eggs. *Received 7 Oct. 1987, accepted 19 Aug. 1988.*

The most accepted hypothesis for the evolution of clutch size in nidicolous birds states that the modal clutch size corresponds to the maximum number of young that can, on the average, be fed and raised (Lack 1947). An offshoot of this hypothesis may explain the evolution of clutch size in the Columbiformes, a group with little or no intraspecific variation in clutch size. With the exception of Apterygiformes, Columbiformes are the only land birds in which no species has a typical clutch size of more than two eggs. With their rapid growth rates (Vandeputte-Poma 1980), columbids are a conspicuous exception to the usual avian pattern of slow growth with small clutches (Ricklefs 1968). Rapid growth appears to be facilitated by the capacity, unique among birds, to produce crop milk which is the exclusive food of 1-4-day-old nestlings (Mirarchi and Scanlon 1980, Vandeputte-Poma 1980).

Crop milk is produced by both males and females. It consists of desquamated cells sloughed off from the germinal epithelium of the crop (Beams and Meyer 1931, Patel 1936). Crop milk is rich in proteins and lipids and contains an uncharacterized growth-promoting factor (perhaps digestive microflora) (Pace et al. 1952, Hedge 1972).

The two exceptional features of columbid reproductive biology, a clutch size of one or two (depending upon the species) and crop-milk production

<sup>1</sup> Bell Museum of Natural History, Dept. of Ecology and Behavioral Biology, Univ. Minnesota, Minneapolis, Minnesota 55455. (Present address: Dept. Zoology, Connecticut College, New London, Connecticut 06320.)

probably are related. Lack (1947:310) noted that the Columbidae are an exception to the usual pattern of seasonal variation in clutch size and that crop-milk production would not be expected to vary with daylength. He regarded crop milk as one of "a number of physiological adaptations [that] are associated with raising a family of two" and that have resulted in reduced plasticity of clutch size (Lack 1948:32).

I tested the crop-milk limitation hypothesis in a wild population of Mourning Doves. I created broods of three, both early in the nestling period when the young are dependent on crop milk and later in the period when the young are fed seeds and crop milk. Three predictions follow from the hypothesis: first, few, if any, broods will produce three fledglings. Second, nestlings in broods of three will have reduced growth rates relative to normal broods of two. Finally, broods of three created after the nestlings have passed the period of total dependency on crop milk will have higher survival and growth rates than broods of three created when the nestlings are wholly dependent on crop milk. An alternative hypothesis is that clutch size is limited by the number of eggs that can be incubated. I manipulated clutch size of Mourning Doves to test this hypothesis.

#### METHODS

I studied Mourning Doves at the J. Clark Salyer National Wildlife Refuge, northern McHenry County, North Dakota, from April through September 1981-83 and in June and July 1984. Two primary study areas were used: a series of three 4.5-ha planted shelterbelts and 20 ha at the refuge headquarters 2 km southeast of the shelterbelts. In 1981, nest searches were also conducted at nearby farm woodlots. Detailed descriptions of the study area are in Blockstein (1986). All trees and shrubs in each shelterbelt were searched weekly for nests. Eggs were aged by candling (Hanson and Kossack 1957). Unless observed, laying and hatching dates were determined by backdating: hatch day was designated day 0. I visited and checked nests every seven days before hatching, within two days after the projected hatch date, and then every three days until fledging.

To test the assumption that Mourning Doves have a determinate clutch size of two, I added a second egg to 23 nests with an incomplete clutch of one fresh egg (<24 h old). The added egg either came from an abandoned nest or was removed temporarily from another active nest. I checked the nest at least 24 h later to determine whether or not the presence of two eggs had inhibited the female from laying a second egg. I removed the "added" egg at this time.

To test whether or not Mourning Doves are able to replace an egg within a clutch, at 30 nests I removed the second egg of the clutch within 10 h after it was laid. These nests were checked again at least 24 h later to see if an additional egg was laid. Most nests were checked again within 7 days. To test the hypothesis that clutch size is limited by the doves' ability to incubate three eggs, at 33 nests I added a third egg within 48 h of clutch completion. The additional egg was always the same age as one of the original eggs in the nest. I checked these nests shortly after the calculated hatching date to see if all had hatched.

To test the crop-milk limitation hypothesis, I added a third nestling at 68 nests. Each nestling was within one day of age and similar in size to the original nestlings. Whenever possible, I altered the brood so that there were two younger nestlings and one older nestling.

This minimized the cases where the smaller nestling was at an immediate competitive disadvantage. Sometimes one nestling was removed from the nest and two transfers added to make a brood of three. The transfers were not always younger than the original nestlings. Generally, only one pair of broods was available for transfer on any day, but, if several choices were available, I tried to create the best match among similar-sized nestlings. To minimize the chances of nestlings falling from the nest, I placed the extra nestlings only in large nests or in nests in wire baskets, which were used for nesting by a few pairs. Although Mourning Doves that hatch early in the nesting season may gain weight more slowly than later nestlings (Holcomb and Jaeger 1978), less than 10% of the transfers were made during the first month of the season.

I divided the sample of experimentally enlarged broods according to nestling age: (1) early addition (3-E): all nestlings  $\leq 4$  days old ( $N = 49$ ) and (2) late addition (3-L): at least one nestling 5–8 days old ( $N = 19$ ). Broods of three created by clutch manipulation or addition of pipping eggs and nests with an unmanipulated clutch size of three were included in the 3-E group for analysis of growth rate. Nests that I found containing three eggs were analyzed separately for nest success. These large clutches probably resulted from laying by more than one female (Weeks 1980, this study).

Every 3 days I measured the nestlings in experimental (both additions and removals) and unmanipulated broods of one, two, or three young. Broods of one created by removal and broods in nests where only one nestling hatched did not differ in growth rates and were combined for comparison with other brood sizes. Nestlings from normal 2-young broods were considered controls. I made 14 exchanges between same-age broods of two young, but discontinued this because there was no evidence that adults distinguished between transfers and their own young.

I weighed nestlings to the nearest 0.5 g using Pesola scales. Total length, natural (unflattened) wing chord, tail length, and length of the sixth primary were measured to the nearest mm. The proportion of seeds and milk in the crop was estimated by external massage. I used plumage development, opening of the eyes, and remission of the egg tooth as aging criteria (Hanson and Kossack 1957). Nestlings were marked on the feet with a colored marking pen and later banded for individual identification. To avoid inducing premature fledging, I usually measured nestlings only through 10 days of age.

I used a jackknife procedure to create Richards growth curves (Richards 1959) as modified by Bradley et al. (1984). This technique combines repeated measurements of individual nestlings with cross-sectional (grouped) data on age-classes to create a composite curve for each brood-size treatment group. Because the nestlings added late in the nesting cycle were not measured separately on days 0–4 when they were in broods of two, measurements from control broods of two on days 0–4 were combined with measurements from 3-L broods, which started at day 5. This data set represented the 3-L group for analysis of growth rates. Growth for each treatment group is expressed as the sum of a smooth growth curve plus its residuals. The curve represents the major trend. The residuals incorporate short-term deviations from this trend. The curve was calculated as:

$$W = A(1 + (M - 1)e^{-K(T-J)})^{1/(1-M)} \quad (1)$$

Where:

- T = time of measurement (age of the organism)
- W = size of the organism at time T
- A = asymptotic size after growth is completed
- K = a growth constant (describes the rate of growth)
- J = time to reach the inflection point in the curve
- M = a shape constant (describes the shape of the curve)

The parameters A, K, J, and M are used to fit the curve and to calculate summary statistics with 95% confidence intervals for each treatment group (Bradley et al. 1984). The statistics are asymptotic size (A), weighted mean growth rate or slope at inflection (R), percentage of asymptotic size at inflection (P), and time to grow from 10–90% of asymptotic size (G). Following Bradley et al. (1984), these statistics are calculated as follows:

$$A = \text{the raw parameter value from the curve}$$

$$R = K/M \quad (2)$$

$$P = M^{1/(1-M)} \quad (3)$$

$$G = \ln((1 - 0.10^{1-M})/(1 - 0.90^{1-M}))/K \quad (4)$$

Mourning Doves fledge at about half of adult size (McClure 1943) and growth curves have not leveled off by the time of fledging at day 14, so measurements of known-age fledglings from broods of two were included in the data set (*sensu* Bradley et al. 1984). These individuals were captured in nets and walk-in funnel traps (Reeves et al. 1968, Blockstein 1986), and most were 20–34 days old when measured. Because there were few recaptures of individuals from broods of one and three (due to small sample sizes), I artificially fixed the asymptotes for these brood sizes at the values determined empirically for broods of two: weight—80 g, total length—175 mm, wing chord—135 mm, tail—100 mm, and sixth primary—73 mm. Thus all curves were forced through the same asymptotes. Because the age at which this value is attained was not fixed, all statistics other than A are valid. This technique is conservative towards differences between groups because it assumes all nestlings will reach the same asymptotic value and compares the time it will take to reach that point.

The confidence intervals for the growth statistics are asymmetrical, and, it is not always possible to compare treatments by looking for means that are outside the 95% confidence interval of the other group. "Borderline" cases may exist, such as when the mean of the group with the larger variance is outside the confidence interval of the group with the smaller variance, but not vice versa. To compare treatment groups for these cases, I used a multiple comparison technique (Gabriel 1978) modified by Hochberg et al. (1982), which is similar to comparing multiple treatment means in an unbalanced one-way ANOVA. I calculated "uncertainty intervals" around the sample means as  $\pm 1/4$  of the width of the 95% confidence intervals (David Bradley pers. comm.). This allows a graphical examination of the growth statistics and provides an approximate test at  $P = 0.05$ . Any pair of sample means is significantly different if their uncertainty intervals do not overlap (Hochberg et al. 1982). Significance levels for all tests are set at  $P = 0.05$  unless stated otherwise.

## RESULTS

*Clutch size and success of supernormal clutches.*—Of 1203 nests where clutch size was known, 1169 (97.2%) had 2 eggs. Six (0.5%) 1-egg clutches may have been incomplete or the result of partial predation. Nests that contained 3 eggs ( $N = 24$ , 2.0%) and 4 eggs ( $N = 4$ , 0.3%) probably resulted from more than one female's laying in a nest (see below; Weeks 1980). Four additional 3-egg nests were found on farm woodlots outside the main study area.

All eggs were laid within 4 days at each of two 4-egg nests. At one of these, all eggs pipped within 4 days, but only three hatched. At the other, three hatched within 2 days, but the fourth was infertile. Two nestlings fledged from each of these nests. At another nest with 4 eggs, there were



2 weeks between two 2-egg "clutches." Two eggs hatched on the same day; another was developing when collected, and the fourth was infertile. At the fourth nest, all 4 eggs were present when the nest was found, but none showed any development 12 days later.

Of 3-egg nests where the laying interval was known ( $N = 20$ ), all eggs were laid within 3 days at 6 nests (30%), 4–5 days at 6 nests (30%), 6–8 days at 4 nests (20%), and 9–12 days at 4 nests (20%). All three eggs hatched at 9 of 18 nests where at least one egg hatched. Two eggs hatched, and the third was near hatching at three other nests when they failed. Three nests had at least one infertile egg. At two nests, the first two eggs hatched, but the third, which was laid much later, never hatched. At one nest, one egg hatched, one fell out of the nest, and the third developed almost to term, but never hatched.

Three young fledged at only 1 of 9 nests where three eggs hatched, although another had nestlings aged 5, 6, and 7 days when last visited. Two young fledged at two nests where the youngest nestling died. One nest was not checked again. No young fledged from the other five nests because of nestling death and predation.

*Nestling diet.*—Crops of nestlings contained almost no seeds during days 0–3, an increasing proportion of seeds from days 4–8, and almost entirely seeds beginning at day 8.

*Determinate laying.*—The female laid her own second egg at 19 of 23 nests where a second egg had been added to an incomplete clutch. One nest was abandoned immediately, and at one the female probably did not lay a second egg. Two nests were destroyed by predators.

No replacement eggs were laid at nests where the second egg had been removed. Fifteen pairs continued to incubate the remaining egg although two nests were abandoned after the second nest check. One nest was abandoned immediately and predation occurred at 14 other nests before they were checked.

*Incubation limitation.*—Eggs hatched at 17 nests where a third egg had been added: all three at 9 nests, two at 5 nests, and one or two at 3 others. Causes of hatching failure included: failure to begin development (3 eggs), embryo death (2 eggs), and death during pipping (1 egg). At least half of the eggs that did not hatch were the eggs that had been transferred. Seven clutches were abandoned and predators destroyed seven others.

*Fledging success.*—All three young fledged at 31% of the early additions and 42% of the late additions ( $\chi^2 = 0.57$ ,  $P > 0.25$ , Table 1). Apart from predation, all the young died at 8 (16%) 3-E nests, including two where the female abandoned, but at no (0%) 3-L nests. One or two nestlings died at 17 (35%) 3-E and at 7 (35%) 3-L nests. Both young fledged at about 60% of the control (two nestling) nests.

TABLE I  
OUTCOME OF ADDING A THIRD NESTLING TO BROODS OF TWO

Outcome	3-E <sup>a</sup> No. nests (%)	3-L <sup>b</sup> No. nests (%)
Three fledged	15 (31)	8 (42)
Two fledged	11 (22)	3 (16)
One fledged	4 (8)	3 (16)
All died in nest	8 (16)	0 (0)
Some died in nest before predation	4 (8)	2 (11)
Predation on all	7 (14)	3 (16)
Total nests	49	19

<sup>a</sup> Third nestling added on days 0-4.

<sup>b</sup> Third nestling added on days 5-8.

Nests where a third nestling was added produced a greater average number of fledglings than did broods of two, both for successful nests ( $\bar{x} = 2.36$  and  $1.73$  for broods of three and two, respectively,  $t_{36} = 3.37$ ,  $P = 0.002$ ) and for all nests ( $\bar{x} = 1.71$  and  $1.08$ ,  $t_{38} = 3.18$ ,  $P = 0.003$ ). Early and late additions did not differ significantly in the average number of fledglings either for successful nests ( $\bar{x} = 2.37$  and  $2.36$  for 3-E and 3-L, respectively,  $t_{13} = 0.04$ ,  $P > 0.50$ ) or for all nests ( $\bar{x} = 1.45$  and  $1.74$ ,  $t_{18} = 0.83$ ,  $P > 0.40$ ).

The relative ages of nestlings within the enlarged broods affected the prospects for survival. Where there was one older nestling and two same-age younger nestlings, all three fledged at 13 of 21 nests, but where there were two same-age older nestlings and one nestling a day younger than the others, all three fledged at only 1 of 7 nests ( $\chi^2 = 4.76$ ,  $0.025 < P < 0.05$ ). Individuals that died, either from starvation or falling out of the nest, included 13 that had originally been the youngest or smallest, six that had been the oldest or largest, and nine that were intermediate.

*Nestling weight.*—Nine and 10-day-old nestlings in broods of two ( $\bar{x} = 61$  g) were significantly heavier than 3-E nestlings ( $\bar{x} = 48$  g) even when the effect of differing amounts of food in the crop was removed by covariance analysis ( $F_{1,46} = 11.02$ ,  $P = 0.002$ ). Nine and 10-day-old nestlings in 3-E and 3-L broods did not differ in weight or in any linear measurement. Seven (17%) 3-E nestlings weighed  $< 35$  g and were considered "runts." Runts occurred in 47% of the 3-E broods that fledged three young ( $N = 15$ ).

*Growth rates.*—Richards growth curves were generally lower for 3-E broods than for broods of one and two, which were very similar (Figs. 1, 2). Broods of 3-L were intermediate, but closer to controls. Curve shape

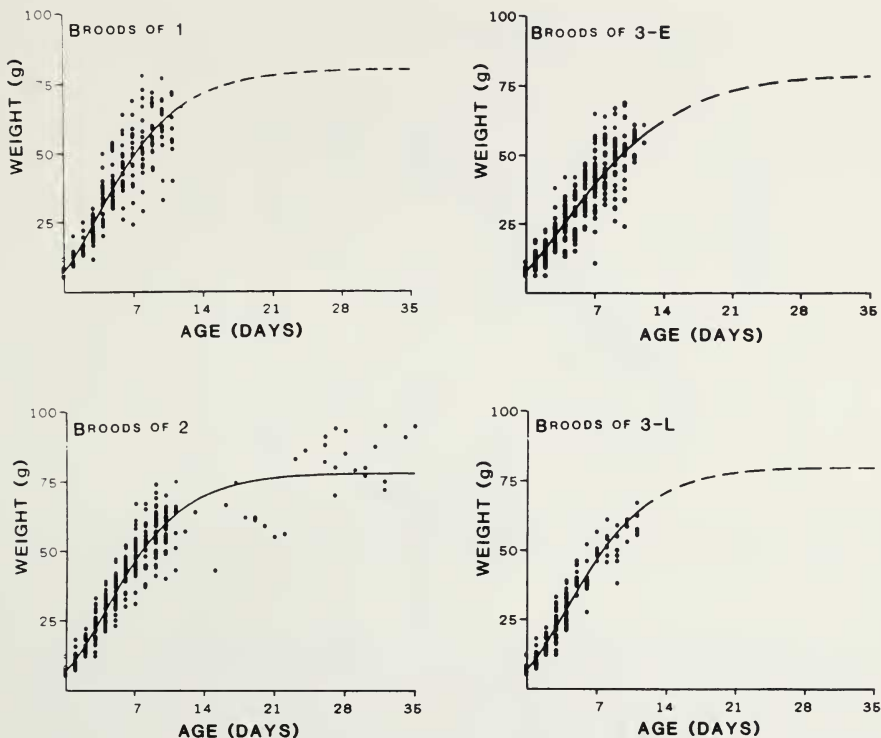


FIG. 1. Richards growth curves of weight for broods of different sizes.  $N = 10$  (brood size 1); 178 (brood size 2); 118 (3-E); 24 (3-L). 3-E and 3-L broods were created by adding a third nestling at days 0-4 and 5-8, respectively.

varied considerably, depending upon the feature measured. Broods of 3-E showed the smallest values of  $M$  (shape) and  $K$  (growth constant) for all measurements except total length. Broods of 3-L had the smallest values of  $M$  and  $K$  for total length and had lower values of  $K$  than broods of two for all measurements. This represents an "incretion" of the growth curve shape as the shape shifted to lower values with presumably greater stress (Brisbin et al. 1986).

Weighted mean growth rate ( $R$ ) and growth period ( $G$ ) were derived from the growth constant in different ways. The percentage of asymptote at inflection ( $P$ ) depends entirely on the shape of the curve. Each is a measure of growth speed.

One-nestling broods did not differ from broods of two in growth statistics for any linear measurement (Fig. 3), but growth rate for weight was marginally lower ( $P = 0.05$ ) than for controls (Fig. 3).

For weight, early additions (3-E) differed from controls for growth pe-

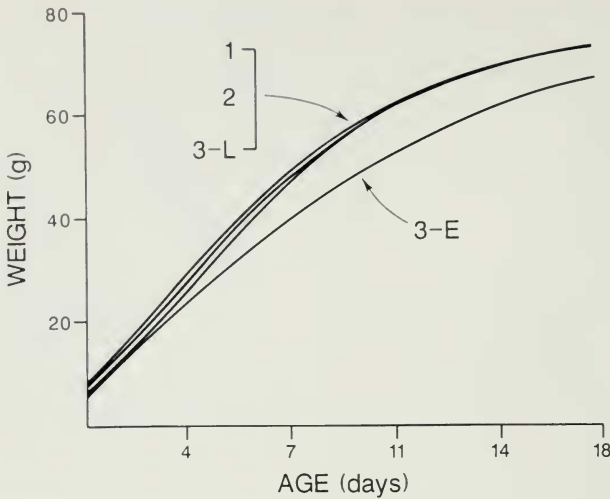


FIG. 2. Richards growth curves of weight for broods of different sizes. Curves taken from Figure 1.

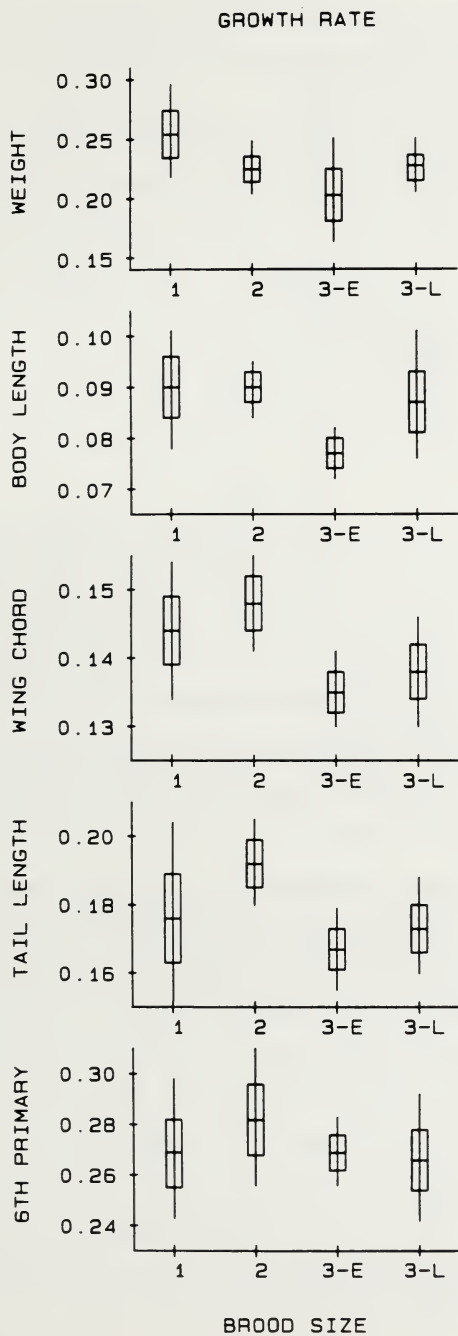
riod and marginally for percentage of asymptote at inflection ( $P = 0.05$ ), but not for growth rate. In all cases, young in the 3-E broods grew more slowly (Fig. 3). That 3-E broods differed from controls in growth period but not in growth rate may have resulted because growth period is more sensitive to changes in shape. The shape parameter of the controls (0.965) was 40% greater than that of 3-E broods (0.691), an indication that weight of 3-E broods began to level off sooner. Weights of late addition broods (3-L) showed the greatest variance and did not differ from controls in any growth statistic. The only difference in weight between 3-E and 3-L broods was that 3-L had a shorter growth period.

For linear measurements, 3-E broods had slower growth rate and longer growth period than controls for three of four features (all but sixth primary) (Fig. 3). There were no differences in percentage of asymptote at inflection. Broods of 3-L had slower growth rate and longer growth period than controls for two measurements (Fig. 3). Early (3-E) and late (3-L) additions

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 FIG. 3. Effect of brood size on nestling growth: weighted mean growth rate ( $R = K/M$ ) from the Richards curves. The horizontal lines are 95% confidence intervals. The boxes are comparison intervals. Any comparison intervals that do not overlap are significantly different at  $P = 0.05$ . The vertical lines are treatment means. The effect of brood size on growth period ( $G$ : time in days to grow from 10–90% of asymptote) is similar and is not shown.





differed only in growth rate and asymptotic percentage for total length. The 3-L group, although intermediate between the 3-E and controls, was usually more similar to the controls.

In broods of two, position within the brood did not affect growth. Older and younger nestlings differed in only one growth statistic (growth period for wing chord); in this case, the younger nestlings grew faster.

There was considerable variation in growth among the 3-E nestlings. There was a preponderance of "runts," some of which died before reaching fledging age. Other 3-E nestlings grew at rates comparable to controls. The oldest and middle nestlings did not differ in growth rates for weight. Nestlings that were originally the youngest or smallest had a slower growth rate but a higher percentage of asymptote at inflection. The growth period did not differ according to position within the brood (Fig. 4). Thus, the effect of position on growth rates was equivocal for 3-E broods.

#### DISCUSSION

*Determinate laying.*—Clutch manipulations verified that Mourning Doves are determinate layers with a clutch size of two. Addition of an egg did not prevent females from laying a second egg nor did removal of the second egg induce the laying of a third egg. These results coupled with the wide variation in laying dates within supernormal "clutches" support Weeks' (1980) hypothesis that enlarged clutches resulted from more than one female's laying eggs in a nest.

Invariance of clutch size in Mourning Doves and other columbids implies strong selection against a 3-egg clutch. This could result from an inability to incubate three eggs or an inability to feed adequately and fledge three young.

*Incubation limitation.*—I found that Mourning Doves can incubate 3-egg clutches, both manipulated and unmanipulated, although hatching success was reduced. However, hatching success at unmanipulated nests with three eggs is expected to be less than 100% because the third egg often is laid several days after incubation begins. In my experiments, chilling of the transferred eggs may have reduced hatching success. In studies where several 3-egg nests were found (not including nests where no eggs hatched), all three eggs hatched at 25–67% of the nests (range of  $N = 8-22$ ) (McClure 1943, Quay 1951, Klataske 1966, Olson 1980). Burley (1980) found that Rock Dove (*Columba livia*) nests given a third egg had identical hatching success to 2-egg nests. Westmoreland and Best (1987) manipulated clutch size in Mourning Doves and also concluded that incubation ability is unimportant as an ultimate factor limiting clutch size to two in columbids.

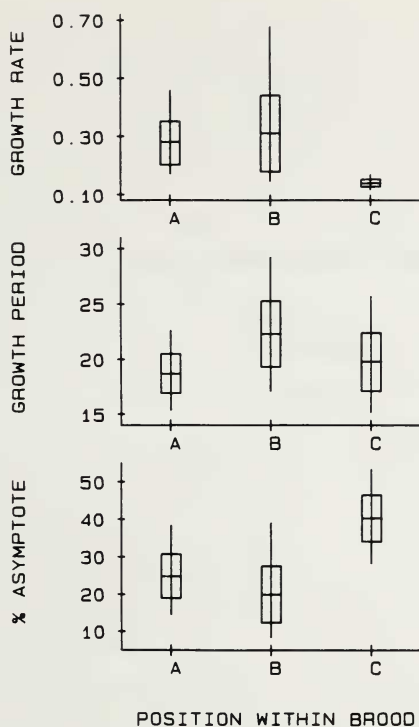


FIG. 4. Effect of position within 3-E broods on nestling weight: growth parameters from Richards curves. Position number refers to relative age or initial size within the brood (position A is the oldest or largest). Symbols are as in Figure 3.

*Fledging success.*—Three young fledged from only one unmanipulated nest in this study. At least one nestling (usually the youngest) died at 6 nests where three eggs hatched. McClure (1943) reported three fledglings at 8 of 15 nests where three eggs hatched. According to the crop-milk limitation hypothesis, the poor fledging success of supernormal broods is due to the parents' inability to produce adequate crop milk for three nestlings. My experiments tested the predictions of this hypothesis: that fledging success would be very low in broods of three, that growth rates would be reduced in broods of three, and that these effects would be more pronounced in broods of three created when the young are crop-milk dependent (3-E) than in broods of three created when the young are being weaned from crop milk (3-L).

Fledging success of experimental broods, although lower than control broods, was better than expected, with three fledglings at 38% of the

experimental broods. Broods of three produced more fledglings per nest than did broods of two. Although death of all three nestlings occurred only among 3-E broods, 3-E and 3-L broods did not differ in fledging success. Wood Pigeons (*Columba palumbus*) (Murton et al. 1974) and Rock Doves in an outdoor aviary (Burley 1980), but not Mourning Doves (Westmoreland and Best 1987), also showed reduced fledging success in experimental broods of three compared with controls.

*Growth rates.*—Survival to fledging may not be a sufficient criterion for evaluating the success of nests with three young. Young fledged at abnormally small size may be less likely to survive to reproductive age. In Wood Pigeons, experimental broods of three fledged at lower weights and had lower fledging success compared with broods of one or two; they also appeared to suffer increased post-fledging mortality ( $P = 0.10$ ) (Murton et al. 1974). Based on these results, Murton et al. (1974) concluded that pairs could, on the average, leave more progeny by producing two nestlings than three.

Reduced growth rates in crop-milk-dependent young have also been found in artificially enlarged broods of Mourning Doves (Westmoreland and Best 1987), Wood Pigeons (Murton et al. 1974), and Rock Doves (Burley 1980). The mean brood weight at 9 and 10 days was only 18% higher for 3-E broods than for controls as opposed to the 50% increase expected if the adults were able to provide enough food for broods of three. Even if adults could gather extra seeds to feed older nestlings in an expanded brood, they are unlikely to be able to increase their production of crop milk. The first few days of life, during which the young are fed only crop milk and have among the fastest growth rates of any bird (Riddle 1928, Riddle et al. 1932) are apparently critical to reaching normal size (Murton et al. 1974, Burley 1980, Westmoreland and Best 1987). The same conclusion can be drawn from experiments showing that a single parent is unable to raise two nestlings until after the crop-milk stage (Haas 1980).

*Crop-milk limitation.*—The significantly reduced growth in 3-E broods supports the crop-milk limitation hypothesis. The nonsignificant tendency toward reduced growth in the 3-L group is suggestive that there may also be difficulty in providing food for three nestlings beyond the crop-milk stage (cf. Westmoreland and Best 1987). Thus it is unlikely that parental feedings of seeds can compensate for the stunting caused by crop-milk limitation. All brood-size experiments in columbids show that limits on crop-milk production cause undersize fledglings (Murton et al. 1974, Burley 1980, Westmoreland and Best 1987, this study), which may take longer to fledge and thus have a lengthened exposure to nest predators (West-

moreland and Best 1987), and lower post-fledging survival (Murton et al. 1974). Because these latter attributes are direct results of crop-milk limitation, it is proper to point to crop milk as the key feature that limits clutch size in columbids. Westmoreland and Best (1987) in ascribing clutch-size limitation in Mourning Doves to an interaction of physiological and ecological factors (including crop milk) fail to emphasize that crop-milk limitation may be sufficient as an explanation for the small clutch size in columbids. Ecological factors help to enforce the impact of crop-milk limitation.

The mode of nestling feeding may exacerbate the effects of crop-milk limitation by determining the distribution of food with the brood. Nestling doves feed by inserting the bill into the corner of the parent's mouth and swallowing the crop milk or seeds that the adult disgorges. With a normal brood of two, the parent often feeds both nestlings simultaneously with one on each side. There is no space for a third nestling. If food is limited, there would not be enough food for a third nestling to feed after the first two have finished. The smallest nestling may consistently lose this competition and become a runt, if it lives at all.

The validity of this mechanism is supported by the distribution of mortality within broods of three. The younger nestlings were more likely to die and mortality was more common when one nestling was initially smaller than the other two. Nestlings that died had grown more slowly than those that survived, but growth rates of younger nestlings (as a group) were not consistently lower than those of older nestmates. The nestling showing reduced growth was often the smallest initially both in Wood Pigeons (Murton et al. 1974) and in Mourning Doves (this study). Transferred nestlings fared no worse than their new nestmates in either species, as would be expected if parents rejected unfamiliar nestlings.

*The importance of crop milk.*—The reproductive strategy of Mourning Doves and other columbids features rapid production of multiple broods in a nesting season (Blockstein 1986, Westmoreland et al. 1986). Crop cycles of adults (Mirarchi and Scanlon 1980, Mirarchi et al. 1982) and weaning of fledglings (Hitchcock and Mirarchi 1984, Blockstein 1986) appear to be timed for rapid renesting. A key to this strategy is a relatively short nesting cycle. This is possible because crop-milk production allows rapid growth of one or two nestlings in a brood.

An increased rate of crop-milk production and delivery may be difficult to achieve evolutionarily. The fact that none of the nearly 300 species of Columbiformes has a clutch size larger than two eggs suggests that there is limited plasticity in crop-milk production. If this were not the case we would expect to see a variety of clutch sizes and concurrent variation in



crop-milk production ability among Columbiformes. It is apparently more successful to alter features such as the interclutch interval and the number of broods rather than the rate of crop-milk production and clutch size.

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#### LITERATURE CITED

- BEAMS, H. W. AND R. K. MEYER. 1931. The formation of pigeon "milk." *Physiol. Zool.* 4:486-500.
- BLOCKSTEIN, D. E. 1986. Reproductive behavior and parental investment of Mourning Doves (*Zenaida macroura*). Ph.D. diss., Univ. of Minnesota, Minneapolis, Minnesota.
- BRADLEY, D. W., R. E. LANDRY, AND C. T. COLLINS. 1984. The use of jackknife confidence intervals with the Richards curve for describing avian growth patterns. *Bull. Southern California Acad. Sci.* 83:133-147.
- BRISBIN, I. L., JR., G. C. WHITE, P. B. BUSH, AND L. A. MAYNCK. 1986. Sigmoid growth analyses of Wood Ducks: the effects of sex, dietary protein, and cadmium on parameters of the Richards model. *Growth* 50:41-50.
- BURLEY, N. 1980. Clutch overlap and clutch size: alternative and complementary reproductive tactics. *Am. Nat.* 115:223-246.
- GABRIEL, K. R. 1978. A simple method of multiple comparisons of means. *J. Amer. Stat. Assoc.* 73:724-729.
- HAAS, G. H. 1980. Success of single-parent Mourning Dove nests. *Proc. Ann. Conf. S. E. Assoc. Fish and Wildlife Agencies* 34:426-429.
- HANSON, H. C. AND C. W. KOSSACK. 1957. Methods and criteria for aging incubated eggs and nestlings of the Mourning Dove. *Wilson Bull.* 69:91-101.
- HEGDE, S. N. 1972. Composition of pigeon milk and its effect on growth in chicks. *Indian J. Exp. Biol.* 11:238-239.
- HITCHCOCK, R. R. AND R. E. MIRARCHI. 1984. Duration of dependence of wild fledgling Mourning Doves upon parental care. *J. Wildl. Manage.* 48:99-108.
- HOCHBERG, Y., G. WEISS, AND S. HART. 1982. On graphical procedures of multiple comparisons. *J. Am. Stat. Assoc.* 77:767-772.

- HOLCOMB, L. C. AND M. JAEGER. 1978. Growth and calculation of age in Mourning Dove nestlings. *J. Wildl. Manage.* 42:843-852.
- KLATASKE, R. D. 1966. Mourning Dove nesting success and nest site selection in a sandhill region of Nebraska. *Nebr. Bird Rev.* 34:71-75.
- LACK, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- . 1948. The significance of clutch size. *Ibis* 90:25-45.
- MCCLURE, H. E. 1943. Ecology and management of the Mourning Dove, *Zenaidura macroura* (Linn.) in Cass County, Iowa. *Res. Bull.* 310, Iowa Agr. Exp. Sta. 355-415.
- MIRARCHI, R. E. AND P. F. SCANLON. 1980. Duration of Mourning Dove crop gland activity during the nesting cycle. *J. Wildl. Manage.* 44:209-213.
- , F. C. GWAZDAUSKAS, AND R. L. KIRKPATRICK. 1982. Gonadal and hormonal characteristics of captive adult Mourning Doves during the nesting cycle. *Theor. Population Biol.* 18:683-695.
- MURTON, R. K., N. J. WESTWOOD, AND A. J. ISAACSON. 1974. Factors affecting egg-weight, body weight, and moult of the Woodpigeon (*Columba palumbus*). *Ibis* 116:52-73.
- OLSON, T. E. 1980. Mourning Doves and land use changes in eastern Colorado. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.
- PACE, D. M., P. A. LANDOLT, AND F. E. MUSSEHL. 1952. The effect of pigeon crop-milk on growth in chickens. *Growth* 16:279-285.
- PATEL, M. D. 1936. The physiology of the formation of "pigeon's milk." *Physiol. Zool.* 9:129-152.
- QUAY, T. L. 1951. Mourning Dove studies in North Carolina. Report on Federal Aid Project 2-R and 26-R, North Carolina Wildlife Resources Commission.
- REEVES, H. M., A. D. GEIS, AND F. C. KNIFFEN. 1968. Mourning Dove capture and banding. U.S. Fish and Wildl. Service Spec. Sci. Report Wildl. 117.
- RICHARDS, F. 1959. A flexible growth function for empirical use. *J. Exper. Biol.* 10:290-300.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419-451.
- RIDDLE, O. 1928. Studies on the physiology of reproduction in birds XXIII. Growth of the gonads and bursa Fabricii in doves, with data for body growth and age at maturity. *Amer. J. Physiol.* 86:248-265.
- , R. W. BATES, AND S. W. DYKSHORN. 1932. A new hormone of the anterior pituitary. *Proc. Soc. Exp. Biol. and Med.* 29:1211-1212.
- VANDEPUTTE-POMA, J. 1980. Feeding, growth and metabolism of the Pigeon, *Columba livia domestica*: duration and role of crop milk feeding. *J. Comp. Physiol.* 135:97-99.
- WEEKS, H. P., JR. 1980. Unusual egg deposition in Mourning Doves. *Wilson Bull.* 92:258-260.
- WESTMORELAND, D., AND L. B. BEST. 1987. What limits Mourning Doves to a clutch of two eggs? *Condor* 89:486-493.
- , AND D. E. BLOCKSTEIN. 1986. Multiple brooding as a reproductive strategy: time-conserving adaptations in Mourning Doves. *Auk* 103:196-203.